

## Non-Molecular Phylogenetic Hypotheses for Ferns

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**ABSTRACT.**—There is a consensus among fern systematists that the eusporangiate ferns, Ophioglossaceae and Marattiaceae, constitute ancient and isolated lineages, the former perhaps allied to progymnosperms. Osmundaceae, Schizaeaceae sensu lato, Gleicheniaceae, Matoniaceae, Cyatheaceae, Dicksoniaceae, and several other small or monotypic families represent early offshoots from the main line leading to higher leptosporangiate ferns, conclusions supported by fossil evidence. Among the higher ferns, there is also general agreement as to the major evolutionary groups (variously assigned subfamilial, familial, or ordinal rank), e.g., the dryopteroid, thelypteroid, blechnoid, asplenoid, polypodioid, dennstaedtioid, and pteridoid/cheilanthoid ferns. There is much less agreement on the origins and interrelationships of these more modern lineages. Highly modified ferns that occupy specialized ecological niches are especially difficult to place in a phylogenetic scheme; these include filmy ferns and heterosporous ferns. Disagreements in various phyletic schemes include the origin of the polypods (and grammitids) from either gleichenioid (exindusiate) stock or from a line leading to the largely indusiate ferns (dennstaedtioid line sensu Holttum, 1949), with sporangia having a vertical annulus. The often-suggested derivation of pteridoid/cheilanthoid ferns from schizaeoid ferns needs reexamination. In recent years, fern systematists have refrained from producing phyletic schemes based on morphological traits, and rigorous cladistic analyses of the Polypodiophyta have never been attempted, perhaps because of a supposed high incidence of reticulate evolution and homoplasy, as well as inadequate and incomplete data sets.

It is the purpose of this paper to summarize ideas on the phylogenetic relationships of ferns, as based on evidence derived from such traditional sources as fossils, comparative morphology, anatomy, and chromosome number. I will approach this topic by first giving a cursory overview of characters that have been employed in the classifications of the last 250 years. These characters form the basis for most of the published evolutionary schemes, including ones by Bower (1926), Holttum (1947, 1949, 1973), Wagner (1969), Mickel (1973, 1974a), and Pichi Sermolli (1977), and also underlie commonly used classifications that lack a schematic depiction of relationships (e.g., Tryon and Tryon, 1982; Kramer in Kubitzki, 1990). The generic sequence proposed by Crabbe et al. (1975) was intended as a filing arrangement for herbaria, but the authors stated that they “incorporate the most recent evidence bearing on phylogeny” (p. 142), so that in fact it qualifies as a classification, more than many that have been advanced. Other phylogenies or classifications incorporating evolutionary principles for all or a portion of the ferns include ones by Ching (1940, 1978), Dickason (1946), Copeland (1947), Alston (1956), Mehra (1961), Nayar (1970, 1976), Bierhorst (1971), and Lovis (1977). These and others were reviewed by Pichi Sermolli (1973).

The various evolutionary schemes cited above are in the form of phyletic trees—dendrograms or sausage-diagrams. The tree by Wagner (1969; Fig. 1)



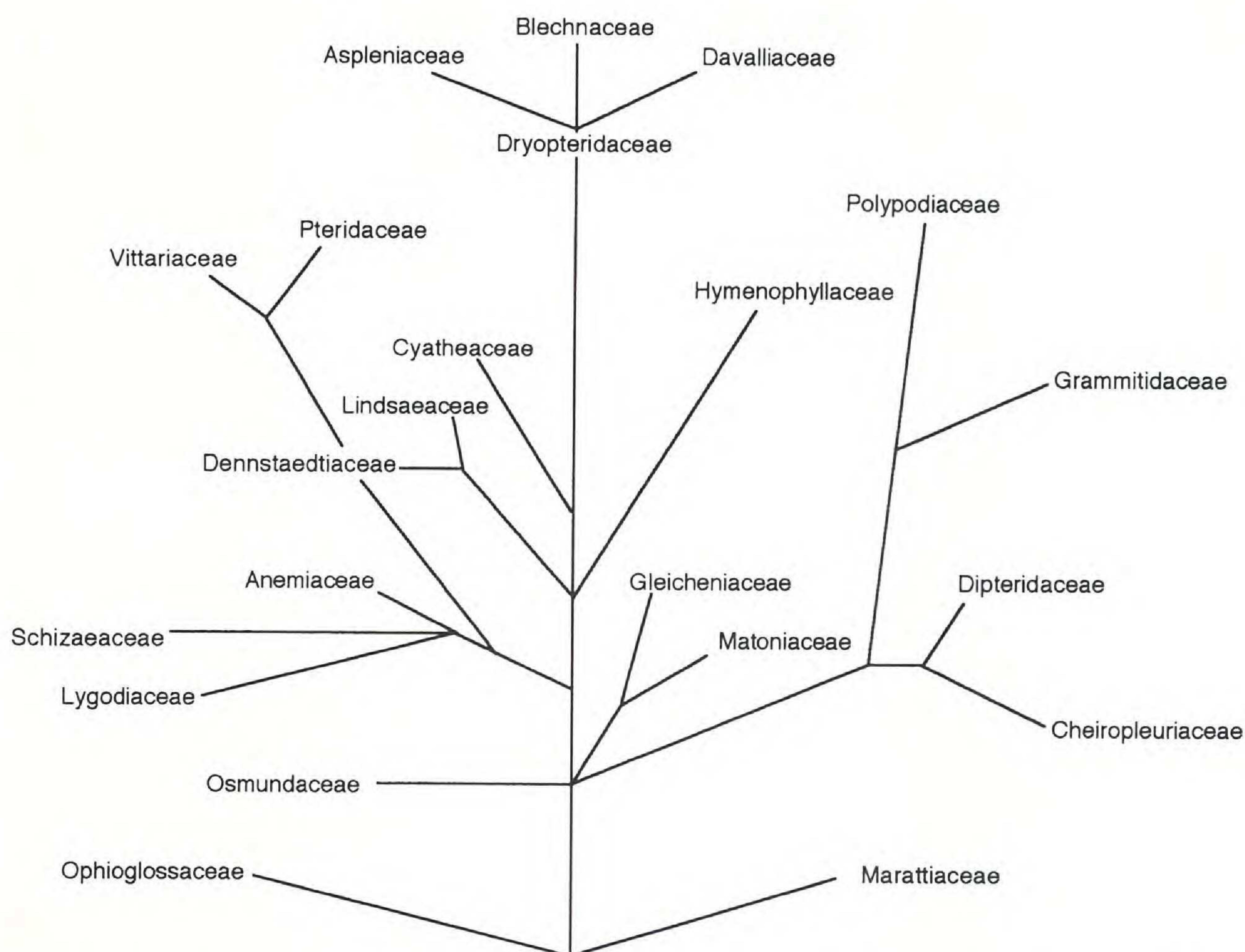


FIG. 1. Evolutionary relationships of ferns, applying the ground plan/divergence method (redrawn from Wagner, 1969). Family names have been substituted for generic names, following the placement of the genera by Kramer (in Kubitzki, 1990).

utilized a more codified approach, the “ground plan/divergence” method. Most of these systems were developed using (admittedly) rather non-rigorous methods, sometimes with little or no explanation given for branching points, relative position, and descendency; in fact, the schemes were intended, as are all phylogenies, as working hypotheses. To date, no one has attempted a cladistic analysis for all of the ferns (Polypodiophyta) using morphological characters.

#### OVERVIEW OF CHARACTERS

The primary sporophytic characters and character states used in construction of most fern classifications and phylogenies are summarized in Table 1. This table was compiled from characters used in previously published classifications and phylogenies (references cited above; also Bower, 1923), as well as lists of character trends in ferns (e.g., Wagner, 1973). Gametophytic characters will not be discussed further here but have also been used to adduce support for various phylogenetic schemes; comparative features of gametophytes have been discussed in several review papers (e.g., Atkinson and Sto-



TABLE 1. Primary sporophytic characters used in construction of classifications and phylogenies of ferns. Other character states are possible, and the sequence of states is not intended to imply evolutionary directionality or phylogenetic trends.

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Habitat: terrestrial/epiphytic vs. aquatic
Root anatomy: polyarch vs. diarch
Rhizomes: habit: creeping vs. ascending vs. erect vs. arborescent
stele: proto- vs. siphono- vs. dictyostelic vs. polycyclic
branching: dichotomous vs. axillary vs. epipetiole
indument: hairs vs. scales
scales: uniformly colored vs. clathrate
tissue: fleshy vs. sclerenchymatous
Stipules: present vs. absent
Frond forms: monomorphic vs. heteromorphic
Stipes: vasculature: 1 trace vs. 2 vs. 3 or more vs. x-shape
sulcation: ungrooved adaxially vs. flattened vs. grooved
articulation: absent vs. present
strengthening tissue: absent vs. collenchyma or sclerenchyma
Blades: architecture: determinate vs. indeterminate
branching: pinnate vs. forking
thickness: multistratose vs. unistratose
indument: glabrous vs. hairs vs. scales
Venation: free (open) vs. anastomosing (closed)
forking vs. pinnate
Idioblasts: absent vs. present
Stomata: anomocytic vs. cyclocytic, copolycytic, etc.
Fertile spikes: absent vs. present
Sori: position: marginal vs. dorsal
shape: round vs. oblong/elongate
paraphyses: absent vs. present (various forms)
Indusia: absence vs. presence
shape: clam-shaped vs. conical vs. cuplike vs. unilateral vs. reniform vs. peltate
orientation: extrorse vs. introrse vs. both
blade margin: unmodified vs. modified and relaxed over sori
Sporangia: capacity: > 1000 vs. 128 vs. 64, 32, or fewer
stalk: absent vs. short-stalked vs. long-stalked
rows of stalk cells: 4+ vs. 3, 2, or 1
grouping: solitary vs. soriate/synangiate vs. coenosoriate or acrostichoid
maturation: simultaneous vs. gradate vs. mixed
Annuli: absence vs. presence
patchlike vs. apical vs. oblique vs. vertical
complete vs. interrupted
Spores: modality: homosporous vs. heterosporous
shape: ellipsoid vs. globose or tetrahedral
marking: monolete vs. trilete
wall: smooth vs. papillate vs. rugose/cristate
color: hyaline vs. variously pigmented vs. greenish
perispore: absent vs. present
Chromosome no.: low vs. high

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key, 1964; Nayar and Kaur, 1971; Atkinson, 1973), and the main evolutionary trends listed by Wagner (1973) and Foster and Gifford (1974). Chemical and molecular characters (e.g., the *rbcL* gene) have just begun to be used to reconstruct fern phylogeny (Hasebe et al., 1994; Wolf et al., 1994).

The first characters to be used in fern classifications involved mostly, sometimes exclusively, reproductive structures of the sporophyte, such as sorus shape and position, and dimorphism of the fertile and sterile leaves (Linnaeus, 1753). Soon thereafter, the nature of the indusium was employed as an important distinguishing character. We now know that these characters must, as all others, be utilized very carefully, selectively, or in conjunction with many others in circumscribing taxa at the higher ranks (families, genera).

Historically, dimorphism alone has been used as justification for generic status, as, for example, with *Marginariopsis wiesbaueri* (Sodirol) C. Chr., which is really a dimorphic *Pleopeltis* (Wagner, 1986; Lellinger, 1989) closely allied to and no doubt congeneric with *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf., a monomorphic species. The dimorphic condition has arisen many times in ferns, in *Tectaria* alone perhaps at least eight times, as exemplified by the segregate genera *Chlamydogramme*, *Dictyoxiphium*, *Fadyenia*, *Hemigramma*, *Luerssenia*, *Quercifilix*, *Stenosemia*, and *Tectaridium*, all included in *Tectaria* by Kramer (in Kubitzki, 1990). Dimorphism occurs in all members of only 3 families of ferns (Plagiogyriaceae, Parkeriaceae, Cheiropleuriaceae; Lomariopsidaceae included in Dryopteridaceae for purposes of this paper), but 20 (of 30) families show moderate to strong dimorphism in at least some of the members, and dimorphism has arisen repeatedly in the large and diverse families Polypodiaceae, Dryopteridaceae, and Pteridaceae.

Sorus position and shape have also been important criteria in generic and family circumscriptions, but this also has led to a false understanding of relationships in many cases. In *Taenitis* (Pteridaceae), sorus position varies from continuous along the veins to marginal, and from more-or-less discrete and scattered to a medial linear band (Holttum, 1968). Similar variation occurs in genera of several other families, including Polypodiaceae (e.g., *Selliguea*), Thelypteridaceae (*Cyclosorus* sensu lato), and Dryopteridaceae (*Nephrolepis*, *Tectaria*).

Indusial characters in ferns are notoriously variable. Complete absence characterizes many primitive genera and families, including Ophioglossaceae, Marattiaceae, Osmundaceae, Schizaeaceae sensu stricto, Gleicheniaceae, and others. Indusial presence characterizes many modern families, but secondary loss of indusia has occurred in many members of Dryopteridaceae (e.g., *Dryopteris*, *Polystichum*, and *Tectaria*), Aspleniaceae (*Pleurosorus*), and other families. In Thelypteridaceae, where indusial presence is probably the ancestral condition, I have estimated that loss of indusia has occurred independently in at least 9 of the 20 subgenera of *Cyclosorus* (Smith in Kubitzki, 1990). Moreover, it is clear that indusia in various families are not homologous; structures called indusia have probably arisen independently along many evolutionary lines. The clam-shaped or conical indusia (involucre) in the filmy ferns may not be homologous with anything else in other families. Similarly, the indusial



flap subtending a single sporangium in *Lygodium* is unique. Indusia in these groups may represent de novo origins of protective structures associated with the sorus, and are not likely to have given rise to other forms of indusia seen in higher ferns. Despite their similar appearance, the cuplike indusia in Cyatheaceae are probably not homologous with similar appearing structures (indusia) in *Woodsia* (Dryopteridaceae), as Bower (1926, p. 309) thought. In the tree ferns, the indusium is thought to have arisen through the progressive development of scales associated with the sorus (Bower, 1928, p. 114; Tryon, 1970), whereas in *Woodsia* the indusium has likely arisen through progressive coalescence of uniseriate hairs (Bower, 1928, p. 117).

In the nineteenth century, systematists began using non-reproductive characters to classify ferns. Presl and Fée utilized characters derived from vegetative parts of the sporophyte, including rhizome, stipe, veins, and indument. Here also there is remarkable homoplasy and variation, even within a genus. Venation in *Hemionitis* varies from essentially free-dichotomous to casually anastomosing, to repeatedly anastomosing and forming polygonal areoles (Mickel, 1974). Similar or even greater variation is known in many fern genera, including *Asplenium*, *Pteris*, *Adiantum*, *Cyclosorus*, and *Tectaria*. In *Cyclosorus*, 10 of the 20 subgenera have both free-veined and anastomosing-veined species (Smith in Kubitzki, 1990).

Blade indument may also be useful in characterizing families and genera, but caveat emptor. The distinction between Dicksoniaceae (with hairs) and Cyatheaceae (with scales and hairs) seems sound, but the discrimination of genera within Cyatheaceae primarily on the basis of scale morphology by Tryon (1970) has been disputed by many (e.g., Holttum and Edwards, 1983; Lellinger, 1988). Nevertheless, characters of the indument are informative when used in conjunction with other characters. In Thelypteridaceae, the range of glands and hairs on the blade (e.g., the stellate hairs of *Goniopteris*) are some of the best characters for discriminating large groups of species.

Sporangia, in particular the nature and orientation of the annulus and stomium, have provided some of the most conserved and consistent characters in ferns, and it is surprising that more attention has not been paid to these structures, both developmentally and as a source of additional taxonomic characters. Casual observation impresses one with the variation in annulus width, number of indurated cells, wall pattern, manner of opening, and stalk characteristics, features surveyed for polypods, grammitids, and vittarioids by Wilson (1959), but unstudied in a comparative way for most other ferns.

In the last 50 years, chromosome number and spore morphology have had a significant impact on classification. Unique base chromosome numbers, e.g.,  $x=22$  in Osmundaceae, are now known to characterize certain groups. Other base numbers are not unique, but are constant within a given family, e.g.,  $x=40$  in Marattiaceae, but also in some members of Dryopteridaceae (*Athyrium*), Aspleniaceae (*Asplenium*), and Blechnaceae (*Salpichlaena*).

Several workers have tried to extrapolate primitive base numbers for extant fern genera through karyotype analysis, and hence to arrive at some prototypal (lower) number for ferns. These attempts have so far failed, primarily because



fern chromosomes show relatively little differentiation, one from another. Recently, isozyme analyses have shown that the fern genome is, in cases studied, highly diploidized (Haufler and Soltis, 1986), and that gene silencing may account for this diploidization (Gastony, 1991). If ferns had lower base chromosome numbers in their history and have arrived at their relatively high numbers through paleopolyploidy, then this is likely to have happened a very long time ago. It would not be surprising if most extant homosporous fern families evolved at the same base numbers that are in existence today.

Spore shape, ornamentation, and fine-structure have been the source of much taxonomic data; unfortunately, characteristics of spores are not often unique. Most genera and families are characterized by having either trilete or monolete spores, but not both. However, both types are known in at least five families, e.g., Dennstaedtiaceae, Grammitidaceae, Vittariaceae, Polypodiaceae, and Thelypteridaceae, although the trilete condition would seem to be derived in the last two, primitive in the first three. Within genera, there is often a great range in wall ornamentation that is useful taxonomically. Few genera or families are unique in their spore ornamentation. Anemiaceae and Lophosoriaceae are exceptional in this regard.

A general conclusion to be reached from the discussion above is that only in rare instances can a single character be used to define adequately a given family or genus of ferns. Most taxa can only be circumscribed in any meaningful way by a constellation of characters. Many of the character states listed in Table 1 have probably arisen in more than one evolutionary line (e.g., character states listed under character 1, 6, 10, 19, 27). That does not, however, preclude their use in classifications when used in conjunction with many other characters. Classifications and phylogenies must be based on as many characteristics as we can muster, or, from the cladistic viewpoint, on as many synapomorphies as possible.

#### RECENT PHYLOGENIES

Detailed comparison of the various fern phylogenies and classifications proposed in the last 50 years is beyond the scope of this paper and probably also unproductive; however, inspection of the most commonly used recent systems (Wagner, 1969, Fig. 1; Holttum, 1973, Fig. 2; Mickel, 1974a, Fig. 3; Pichi Sermolli, 1977, Fig. 4; Tryon and Tryon, 1982; Kramer in Kubitzki, 1990) suggests that there are many more areas of agreement than disagreement. Areas of general accord among these six systems include the following:

1. The Ophioglossaceae and Marattiaceae are only distantly related to the other ferns.
2. About ten families are regarded as "primitive" or ancestral with respect to the higher leptosporangiate ferns. These "primitive" families include the Osmundaceae, Schizaeaceae sensu lato, Gleicheniaceae, Matoniaceae, Dipteridaceae, Plagiogyriaceae, Loxsomaceae, Hymenophyllaceae, Dicksoniaceae, and Cyatheaceae.
3. There are, conservatively, about a dozen families of more advanced po-



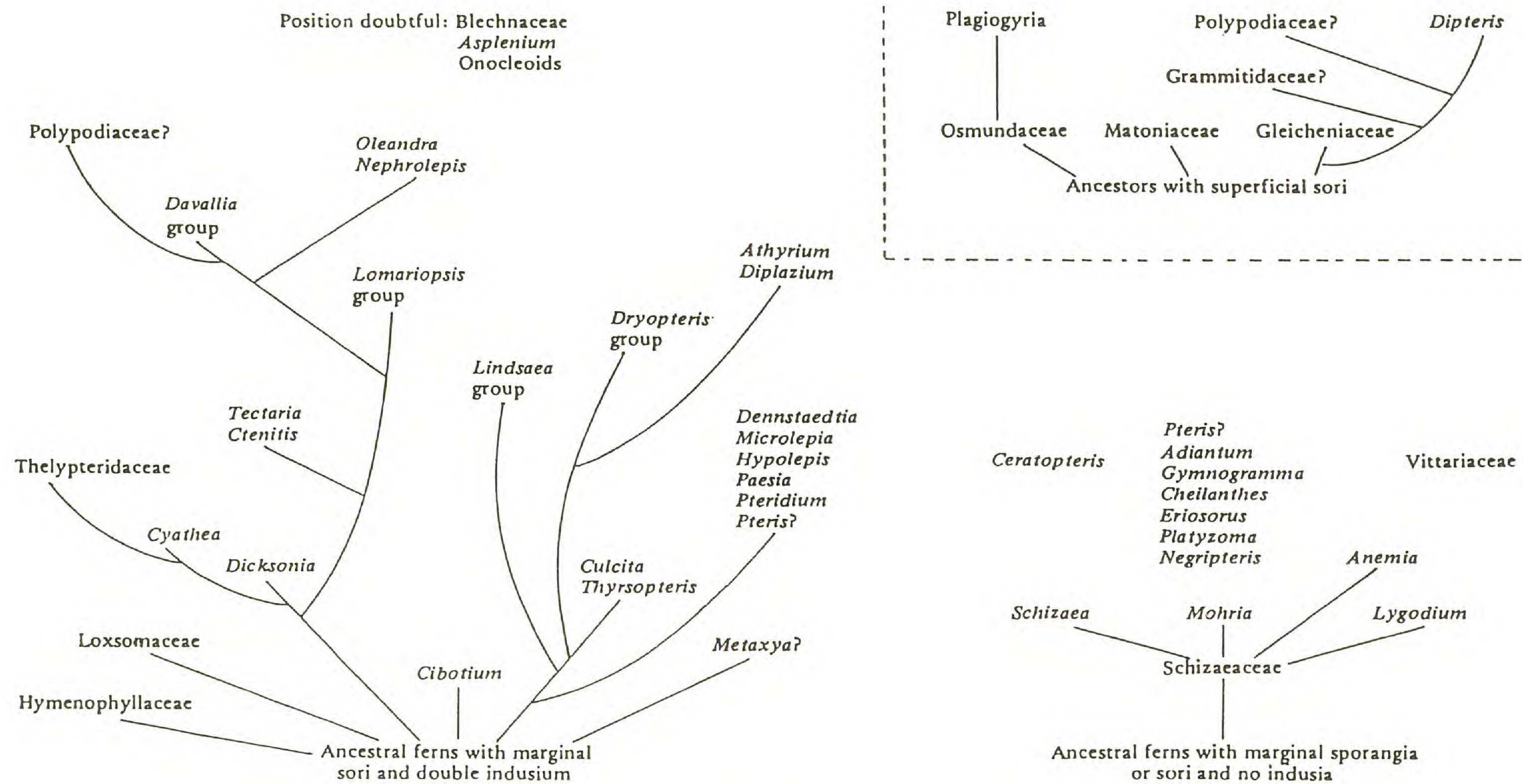


FIG. 2. Phyletic diagram showing possible relationships of ferns (from Holttum, 1973).



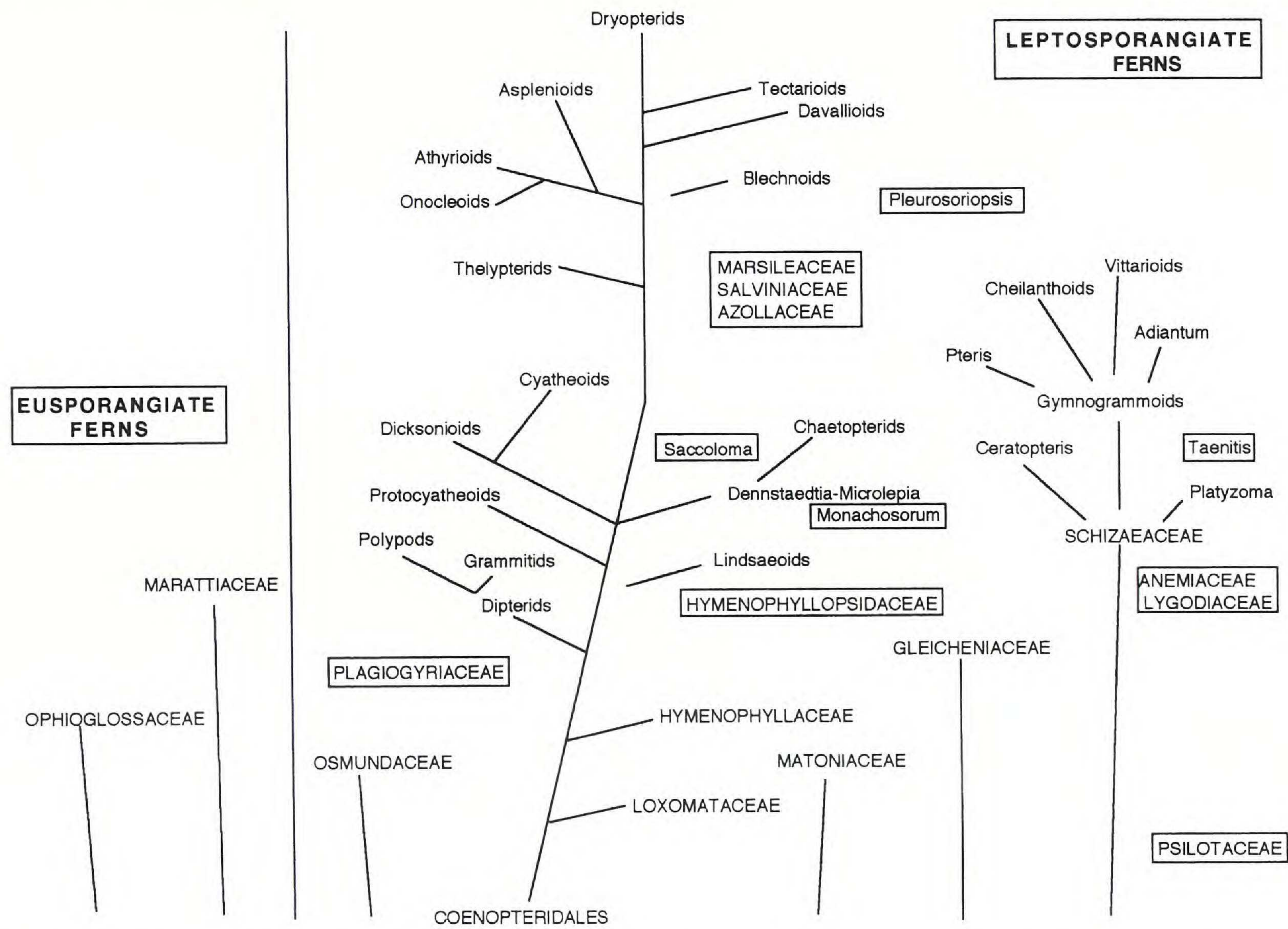


FIG. 3. Phyletic diagram showing presumed relationships of the major groups of ferns (based on Mickel, 1974a; additions shown in boxes).



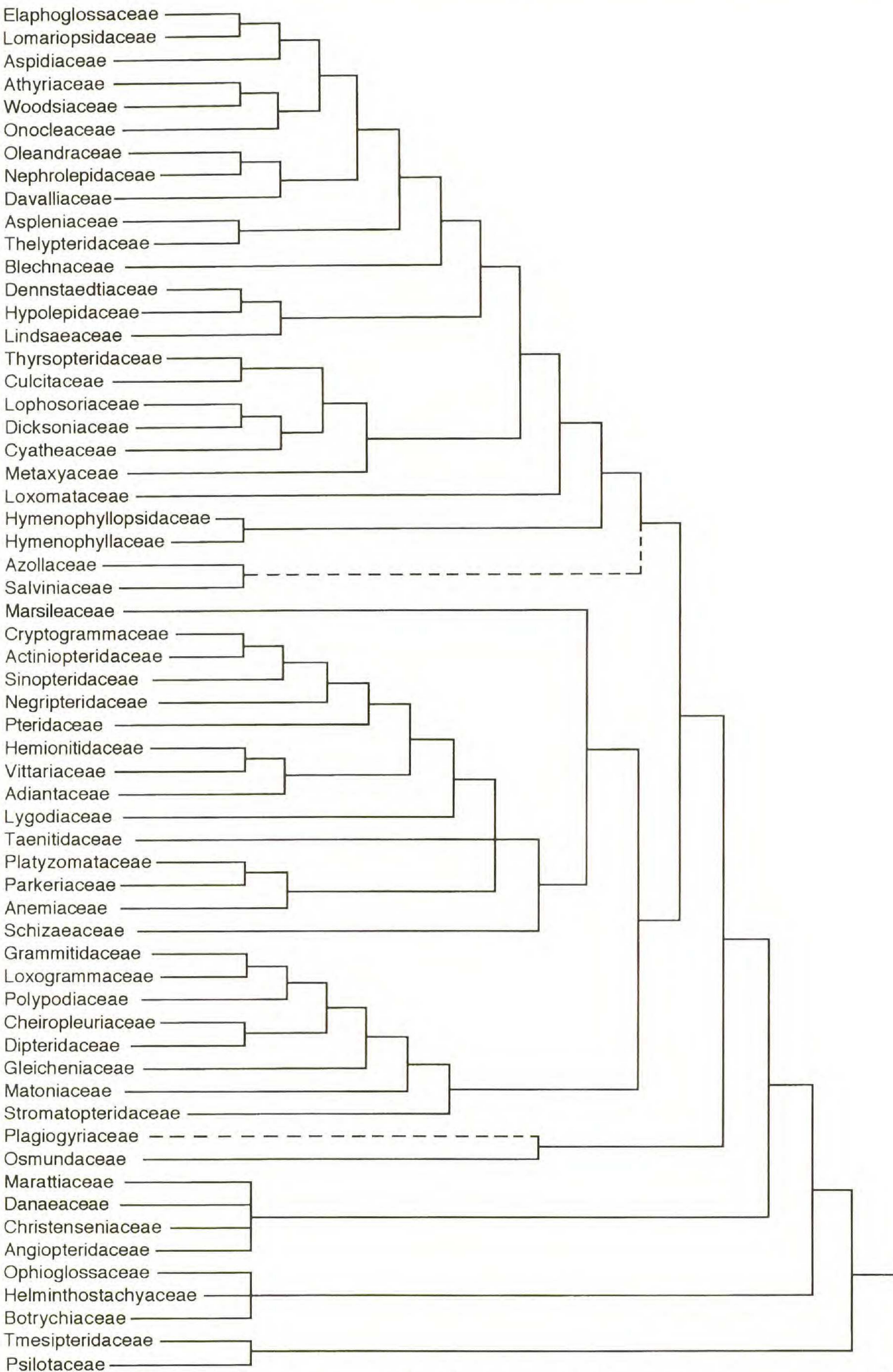


FIG. 4. Phyletic diagram showing presumed relationships of the ferns (redrawn and combined from Figs. 1, 3, 7, and 12 in Pichi Sermolli, 1977). Pichi Sermolli did not explicitly imply evolutionary distance by the line lengths used in his figures, and this rendering does not either. Dashed lines indicate uncertainty by Pichi Sermolli. The family name *Aspidiaceae* used by him is illegitimate; *Dryopteridaceae* is the correct name.



sition, including Dennstaedtiaceae, Pteridaceae sensu lato, Vittariaceae, Polypodiaceae, Grammitidaceae, Thelypteridaceae, Dryopteridaceae sensu lato, Aspleniaceae, Blechnaceae, and two or three heterosporous families. About 30 families are included in this category if a restricted view of family circumscription is adopted (Pichi Sermolli, 1977).

4. The higher leptosporangiate ferns are derived from three or more sources within the lower ferns. For example, the family Pteridaceae is derived from schizaeoid stock in the systems of Wagner (1969), Mickel (1974a), Pichi Sermolli (1977) (Figs. 1, 2, 4), and Lovis (1977). Polypodiaceae and Grammitidaceae originate from gleichenioid progenitors in all of the same systems, except that of Mickel (1974a; Fig. 3). Most of the remaining higher leptosporangiate ferns are derived from dennstaedtioid stock in most systems (Wagner, 1969; Mickel, 1974a; Lovis, 1977; Pichi Sermolli, 1977) (Figs. 1, 3, 4). The system by Holttum (1973; Fig. 2) is exceptional in that it derives the dryopteroids from at least three ancestral sources.

5. Those who commit themselves (most do not) derive the heterosporous families from widely divergent sources (Bierhorst, 1971; Pichi Sermolli, 1977).

#### PRIMITIVE FERN FAMILIES

There is general consensus with regard to the circumscription of the primitive fern families, one of which may not be a true "fern":

1. Ophioglossaceae—This family (given its own order by many and class by some, e.g., Pichi Sermolli, 1977) is now generally considered only remotely allied to the Filicales (e.g., by Wagner, 1964; Kato, 1987, 1988), and some evidence suggests that it may be progymnospermous, perhaps most closely allied to cycadophytes (Kato, 1988; Wagner in Kubitzki, 1990). Evidence for this affinity includes: Presence of a vascular cambium and periderm; eustelic vascular system; tracheids with circular bordered pits; axillary branching; solitary sporangia without an annulus; and non-circinate vernation. Members of the Ophioglossaceae possess many unique synapomorphies, including anomocytic stomata, spikelike sporophores, and conduplicate blades. The fossil record is meager. Spores of a generalized nature have been ascribed to *Ophioglossum* from the Jurassic (see Tryon and Tryon, 1982), but may not be correctly identified. Segregate families are recognized by some systematists (Botrychiaceae, Helminthostachyaceae), but no one has questioned that the family in the broad sense is monophyletic.

2. Marattiaceae—By nearly all workers this family (placed in its own order by many and a separate class by some) is considered an ancient and phylogenetically isolated group (e.g., Pichi Sermolli, 1977; Camus in Kubitzki, 1990) without close affinity to Ophioglossaceae, with which it has traditionally been associated. It is the only other "eusporangiate" family. Evidence for this isolation includes the following traits: Endarch protophloem and protoxylem; multicellular root hairs; mucilage canals in roots, stems, and leaves; massive stipules; dicyclocytic stomata; and tight packing or fusion of sporangia into synangia. The fossil record extends to the Carboniferous with *Psaronius*



(stems), *Scolecoperis* (fertile leaves), and many other genera. Segregate families (Angiopteridaceae, Christenseniaceae, Danaeaceae) are recognized for most genera by some workers (e.g., Pichi Sermolli, 1977), but no one has questioned that the family in the broad sense is monophyletic. Hill and Camus (1986) presented a cladistic analysis, based on morphology and anatomy, that showed that of the genera only *Christensenia* and *Danaea* are monophyletic, and that *Marattia* and *Angiopteris* are paraphyletic.

3. Osmundaceae—This family is considered an isolated and basal offshoot in the filiclean line by nearly all workers. Only the family Plagiogyriaceae has been suggested as being along the same phyletic line. Even though the sporangial development has some features of the so-called “eusporangiate” ferns (several initials, large spore output), the majority of characters (wall one cell thick, patch-like annulus) indicate a closer relationship to the “leptosporangiate” ferns. The fossil record, based in part on the distinctive C-shaped vascular bundles in the stem and stipe bases, extends back to the late Permian. The family is circumscribed similarly by all workers, and usually three genera are recognized.

4. Schizaeaceae sensu lato—By all workers, this family, or group of related families, is considered an early offshoot on the filiclean line. The constituent genera are united because of the similar nature of the sporangia, with an apical or subapical annulus. However, Bierhorst (1971) and others have pointed out that the sporangia of Schizaeaceae sensu lato are really not significantly different from sporangia of Gleicheniaceae or the Coenopteridales. Because the character state differences separating the (usually) four genera are so numerous and striking, many workers now subdivide Schizaeaceae sensu lato into three families: Anemiaceae (*Anemia* and *Mohria*), Schizaeaceae (*Schizaea*, *Actinostachys*), and Lygodiaceae (*Lygodium*) (Bierhorst, 1971; Pichi Sermolli, 1977; Wagner and Smith, 1993), and even *Mohria* has been given family status. These three families differ widely, e.g., in plant habit, chromosome base number(s) ( $x=38$  in *Anemia*, *Mohria*;  $x=77, 93, 94, 103$  in *Schizaea*, *Actinostachys*;  $x=29, 30$  in *Lygodium*), spores, sporangia, vascular anatomy, and gametophytes. In fact, the differences among the genera in Schizaeaceae sensu lato seem larger than among families of higher leptosporangiate ferns. There is no compelling morphological evidence that the five genera even constitute a monophyletic group. Schizaeaceous microfossils (especially the characteristic spores, as in *Anemia*) have been found in the Jurassic and Lower Cretaceous.

Various workers have considered the Schizaeaceae or the family's immediate progenitors to be a possible point of origin for several higher leptosporangiate families, such as Pteridaceae (including Adiantaceae) (Mickel, 1962, 1974a; Wagner, 1969; Holttum, 1973; Lovis, 1977; Kramer in Kubitzki, 1990), Vittariaceae (Wagner, 1969; Holttum, 1973; Mickel, 1974a; Lovis, 1977; Kramer in Kubitzki, 1990), Parkeriaceae (Mickel, 1962, 1974a; Holttum, 1973), and Marsileaceae (Bierhorst, 1971). This postulated kinship is based largely on rather tenuous characters, mainly the globose-tetrahedral spores with trilete aperture, “nodding” vernation, similar stipe vasculature, and asymmetric gametophytes. However, not all members of the families concerned have these characteristics,



and the same characteristics are found in other fern groups. Thus, the evidence for a genealogical linkage seems weak. Moreover, the strikingly different sporangia in the supposed “derivative” genera argue against close phylogenetic relationship.

5. Gleicheniaceae—By most fern systematists, the family Gleicheniaceae is considered a somewhat isolated, monophyletic family, comprising three to five genera, depending on the classification of *Gleichenia*. Fossil records are known from the early Mesozoic.

Several systematists have considered the family, or its immediate ancestors, to be on an evolutionary line leading to other filiclean families, e.g., Matoniaceae (Wagner, 1969; Bierhorst, 1971; Lovis, 1977), Cheiroleuriaceae and Dipteridaceae (Wagner, 1969, Fig. 1; Bierhorst, 1971; Holttum, 1973, Fig. 2; Lovis, 1977), and Polypodiaceae and Grammitidaceae (Bierhorst, 1971; Holttum, 1973, Fig. 2; Lovis, 1977). Others place Gleicheniaceae in a more isolated and dead-end evolutionary position (Mickel, 1974a; Fig. 3).

6. Lophosoriaceae, Metaxyaceae, Dicksoniaceae, Cyatheaceae—These four families can be considered together, because nearly all fern systematists (except Holttum, 1973; Fig. 2) have regarded them as constituting a monophyletic group, either a single family Cyatheaceae (Bierhorst, 1971; Lovis, 1977) or a group of families that have more in common with each other than with any other fern families (Kramer in Kubitzki, 1990); two additional families, Culcitaceae and Thyrsopteridaceae, have sometimes been segregated from Dicksoniaceae (e.g., by Pichi Sermolli, 1977). Most, but not all, are tree ferns, and most have large trunks or at least thick rhizomes with complex stelar anatomy. Sori are marginal or dorsal, discrete, round, and are either exindusiate or indusiate, the indusia clam-shaped, cup-like, or globose. Sporangia have the annulus slightly oblique and just bypassing the stalk. Chromosome base numbers are high, generally from 65 to 69, and spores are trilete. Fossils from the Jurassic appear to be assignable to modern day Cyatheaceae and Dicksoniaceae (Tryon and Tryon, 1982).

7. Hymenophyllaceae—This family is circumscribed similarly by all students of ferns, and is regarded by all phylogenists as highly specialized morphologically and ecologically and without obvious close relatives. Most workers have regarded it as a rather early offshoot from the filiclean line (Wagner, 1969, Fig. 1; Bierhorst, 1971; Mickel, 1974a, Fig. 3; Pichi Sermolli, 1977, Fig. 4), but most, like Kramer (1990) acknowledge that the relationships of Hymenophyllaceae to other ferns “cannot at present be determined”. Pichi Sermolli (1977) argued that some evidence (gametophyte structure, embryogeny, sporangial position) might suggest an affinity to schizaeoid ferns. The soral and indusial structures of Hymenophyllaceae are unique and not clearly homologous with anything else known. Because of the filmy nature of the plants, fossil evidence is scant.

8. Others: Plagiogyriaceae; Loxomataceae; Matoniaceae; Dipteridaceae; Cheiroleuriaceae; Hymenophyllopsidaceae—All six of these families are regarded by systematists as rather isolated and rather early offshoots on the filiclean



evolutionary line. All contain a single genus, with the exception of Loxomataceae, with two genera.

If placed at all, the family Plagiogyriaceae is generally suggested to be possibly allied to Osmundaceae, but Bierhorst (1971) derived it from ancestral cyatheaceous stock, and Ching (1958) suggested Schizaeaceae as possibly related.

The family Loxomataceae, all agree, is an isolated taxon. General similarity in soral structure has caused some to suggest a relationship to Hymenophyllaceae or Cyatheaceae, but little other evidence supports this. Spore morphology and chromosome number are not unlike some members of Dennstaedtiaceae (Tryon and Tryon, 1982). The fossil genus *Stachypteris*, from the Jurassic, has sori that suggest placement in Loxomataceae.

*Cheiropleuria* and *Dipteris*, usually placed in monotypic families, are generally considered to be allied to each other, based on the similar reticulate venation with included veinlets, dichotomous blade branching, stipe vasculature, sporangia, and the same chromosome base number ( $x=33$ ), but there are important differences: spore number per sporangium (128 in *Cheiropleuria*), spore aperture (monolete in *Dipteris*, trilete in *Cheiropleuria*), and rhizome anatomy. Jarrett (1980) presented evidence that linked the two more closely with Gleicheniaceae, rather than Polypodiaceae, with which they have usually been allied (Copeland, 1947; Pichi Sermolli, 1977; Fig. 4).

#### ADVANCED FERN FAMILIES

In the advanced fern families, there is lack of agreement on rank, whether subfamily, family, or order, accorded to groups of related genera, but in general there is agreement with regard to the circumscription of the taxa. Not much evidence exists, from either the fossil record or from comparative morphological studies, as to the interrelationships of the taxa of higher rank (families and orders) or of the genera within the families.

1. Dennstaedtiaceae—The family Dennstaedtiaceae is often defined in a relatively broad sense, to include also Hypolepidaceae, Lindsaeaceae, and Monachosoraceae of other workers. The lindsaeoids and the dennstaedtioids are sometimes given separate tribal (Tryon and Tryon, 1982) or subfamily status (Kramer in Kubitzki, 1990). Some authors segregate *Hypolepis* and its allies (chaetopterids) (Lovis, 1977; Pichi Sermolli, 1977); others include them within the Pteridaceae (Bierhorst, 1971). The dennstaedtioids are united on the basis of the marginal or submarginal sori and often long-creeping, protostelic or solenostelic stems. However, in other characteristics they are very heterogeneous: spore shape; scales vs. hairs; presence or absence of indusia; indusial type; chromosome number. Various relationships have been postulated, including to the cyatheoids (Lovis, 1977; Kramer in Kubitzki, 1990) and dicksonioids (Mickel, 1974a). Others suggest that the family is a basal offshoot from the line leading to all of the higher indusiate, leptosporangiate ferns (Wagner, 1969; Fig. 1) or even the direct ancestor of the bulk of the indusiate ferns (Lovis, 1977).



2. Pteridaceae, Vittariaceae, Parkeriaceae—The family Pteridaceae is usually defined in a relatively broad sense (as by Tryon and Tryon, 1992; Tryon et al. in Kubitzki, 1990; Wagner and Smith, 1993). As such, it is a large, heterogeneous family that includes up to about ten groups sometimes recognized as families by other authors. Among the segregates, the most commonly accepted ones are Acrostichaceae, Actiniopteridaceae, Adiantaceae, Cheilanthaceae, Cryptogrammaceae, Hemionitidaceae, Negripteridaceae, Platyzomataceae, Sinopteridaceae, and Taenitidaceae.

The pteridoid ferns are most often thought to have been derived from Schizaeaceae (Mickel, 1974a, Fig. 3; Lovis, 1977) or from schizaeoid stock (Wagner, 1969; Fig. 1), but the evidence is not very strong (Kramer in Kubitzki, 1990). Supposed affinities are based largely on the lack of a “true” indusium, trilete spores, and general preference for xeric habitats, but the sporangium is more like that of higher indusiate filiclean ferns. *Pteris* itself is disputed as to whether it is more closely allied to the dennstaedtioids or to the cheilanthoids (e.g., by Holttum, 1973; Fig. 2).

By nearly all workers, the family Vittariaceae is considered derived from pteridoids or pteridoid stock (Wagner, 1969, Fig. 1; Bierhorst, 1971; Mickel, 1974a, Fig. 3; Lovis, 1977; Kramer in Kubitzki, 1990). Characteristics that relate the two include chromosome base number ( $x=30$ ), trilete spores, presence of epidermal idioblasts, and exindusiate sori.

*Ceratopteris* is variously included in Pteridaceae (Tryon and Tryon, 1982; Tryon et al. in Kubitzki, 1990), placed in a separate family Parkeriaceae and allied to Anemiaceae (Pichi Sermolli, 1977; Fig. 4), or derived from Schizaeaceae (Mickel, 1974a, Fig. 3; Lovis, 1977). The base chromosome number,  $x=38$  suggests that the relationship to other Pteridaceae is not close.

3. Polypodiaceae, Grammitidaceae—These two families have usually been regarded as derived from gleichenioid stock (e.g., by Wagner, 1969, Fig. 1; Bierhorst, 1971; Holttum, 1973, Fig. 2; Lovis, 1977), or at least exindusiate stock, but a dissenting view was given by Mickel (1974a; Fig. 3), who derived both families from dipteroid stock at the base of the higher leptosporangiate line. Jarrett (1980) effectively refuted a gleichenioid origin and suggested that the polypods and grammitids are more closely allied to higher, indusiate, leptosporangiate ferns. The family Grammitidaceae has usually been thought to be derived from Polypodiaceae, and often included within that family (Tryon and Tryon, 1982; Price, 1983), but Smith (1993) questioned both the closeness of the relationship and the derivation of grammitids from polypods on phylogeographic grounds.

4. Thelypteridaceae—Nearly all modern authors now accept the distinctness and homogeneity of this family, once considered a part of a large and polyphyletic *Dryopteris*. Characteristics uniting the thelypterids include the stipe vasculature (two lunate bundles, in cross-section), the (usual) presence of acicular hairs on the blades, and chromosome base numbers from 27-36 in an almost unbroken sequence. Their affinities have been considered to be with Cyatheaceae by Holttum (1973; Fig. 2) and Lovis (1977), but Smith (in Kubitzki, 1990) offered evidence against this relationship and Mickel (1974a; Fig. 3)



and Pichi Sermolli (1977; Fig. 4) allied the thelypterids with the line giving rise to the higher indusiate families.

5. Dryopteridaceae—The Dryopteridaceae, as broadly defined (as by Tryon and Tryon, 1982; Wagner and Smith, 1993) are the largest and most diverse of the higher leptosporangiate families and include 14 family segregates of other authors. Among the segregates, the most commonly recognized are Athyriaceae, Davalliaceae, Lomariopsidaceae, Nephrolepidaceae, Oleandraceae, Onocleaceae, and Woodsiaceae. Seven others are occasionally recognized: Dictyoxiphiaceae, Didymochlaenaceae, Elaphoglossaceae, Hypodematiaceae, Hypoderriaceae, Peranemataceae, and Tectariaceae. With a broad circumscription, the family Dryopteridaceae is essentially Copeland's (1947) Aspidiaceae, with the removal of Thelypteridaceae and the addition of Davalliaceae. All dendrograms show the family (or its segregates) at the tip of the phyletic tree. Fossils ascribable with certainty to the family are not known until at least the late Cretaceous and do not appear common until the Cenozoic.

6. Aspleniaceae, Blechnaceae—By nearly all recent workers, these two families are regarded as late offshoots from higher filicalean ferns (Wagner, 1969, Fig. 1; Mickel, 1974a, Fig. 3; Lovis, 1977; Pichi Sermolli, 1977, Fig. 4), but their nearest affinities are yet to be determined. Both families are circumscribed similarly by all, with one exception: The inclusion or not of *Pleurosoriopsis* in Aspleniaceae. There is great dispute and difference of opinion with regard to generic delimitation in both families, more so than with genera in most other fern families. Fossils of undoubted Blechnaceae are known from the Paleocene, but have not been found in the Mesozoic (Tryon and Tryon, 1982).

7. Marsileaceae, Azollaceae, Salviniaceae—Historically, the heterosporous fern families were treated as being related and grouped in the same order (Rhizocarpaceae, Hydropteridales). More recently, and in most classifications of the last 50 years, their similarities were thought to be due to convergence, as by Eames (1936), Bierhorst (1971), Pichi Sermolli (1977, p. 407), and Kramer (in Kubitzki, 1990). The family Marsileaceae has usually been regarded as a possible offshoot of Schizaeaceae (Bierhorst, 1971; Pichi Sermolli, 1977, Fig. 4; Lovis, 1977), whereas the Salviniaceae and related Azollaceae are sometimes considered as possibly derived from or related to Hymenophyllaceae (Eames, 1936; Bierhorst, 1971). Characteristics used to support the linkage of Marsileaceae to Schizaeaceae include solenostelic rhizomes, dichotomous venation, and septate trichomes (Tryon and Tryon, 1982). The exciting discovery of the Late Cretaceous fossil genus *Hydropteris*, with characteristics of all three extant heterosporous families (Rothwell and Stockey, 1994), provides strong evidence that the heterosporous ferns are a monophyletic group. Pryer (1993; unpublished data) also has molecular evidence that links the heterosporous ferns. The links of heterosporous ferns to other filicalean ferns are still insufficiently known. Fossils of all three extant families are known from the Cretaceous.



## PROBLEMS

Differences among the various classification schemes and gaps in our knowledge about relationships among fern families and genera can be summarized by posing a number of questions, some already mentioned, questions that are at the core of constructing accurate phylogenetic hypotheses. These problems can be more easily visualized by reference to one of the existing phyletic schemes, e.g., Mickel (1974a; fig. 3), to which several additions (in boxes) have been made.

1. Where goes *Saccoloma*? Usually placed in the Dennstaedtiaceae (e.g., by Kramer in Kubitzki, 1990; Tryon and Tryon, 1982), but chromosome base number ( $x=63?$ ) and spores may indicate a closer alliance with Dicksoniaceae.

2. What are the relationships of *Monachosorum*? Usually allied to the dennstaedtioid ferns. By some, it is placed in a monotypic family Monachosoraceae, with uncertain affinities (Kramer in Kubitzki, 1990).

3. What are the relationships of *Ceratopteris*? By some, included within Pteridaceae, by others regarded as a separate family. Is it closer to Schizaeaceae, as some have suggested? Similar questions could be posed for *Taenitis* and *Platyzoma*, both satellite genera ascribed to Pteridaceae or treated as separate but related families.

4. What are the affinities of *Pleurosoriopsis*? Chromosome base number ( $x=36$ ) and spores (bilateral) could indicate Aspleniaceae, where it was placed by Ching (1940) and Pichi Sermolli (1977), but clathrate scales are lacking, spores are green, and gametophytes are gemmiferous. Hairs are unlike those of Grammitidaceae, where it was placed by Tryon and Tryon (1982). A close relationship with Pteridaceae (where placed by Copeland, 1947) seems unlikely. Kramer (1990) categorized it as "Incertae sedis". It has been placed in a separate family, Pleurosoriopsidaceae.

5. What are the relationships of Hymenophyllopsidaceae? Doubtfully with Hymenophyllaceae, as some have suggested; perhaps with Dennstaedtiaceae? No chromosome counts have been published.

6. What are the relationships of the Hymenophyllaceae? Some have suggested Dennstaedtiaceae, but the phylogenetic position is generally acknowledged as obscure. The group's sorus structure is unique.

7. What is the relationship, or lack thereof, between Polypodiaceae and Grammitidaceae? Some include the constituent genera in the same family (Tryon and Tryon, 1982; Price, 1983; Lellinger, 1989). To me, they seem not very close, with Grammitidaceae showing evidence of being older (Smith, 1993).

8. What are the relationships of Plagiogyriaceae? The default candidate for nearest ally is Osmundaceae, but the relationship cannot be close.

9. What are the relationships and origin of the heterosporous fern families, Marsileaceae, Azollaceae, and Salviniaceae? Are the Marsileaceae derived from schizaeaceous stock, as some have suggested (Kramer in Kubitzki, 1990)?

10. What are the relationships of Psilotaceae? With *Stromatopteris*, as sug-



gested by Bierhorst (1971), or are the whisk ferns an isolated offshoot well removed from the ferns, with still obscure relationships (Wagner, 1977)?

11. What are the relationships of Thelypteridaceae? With Cyatheaceae, as suggested by Holttum (1947, 1949), or with Dryopteridaceae or Aspleniaceae, as I and some others believe?

12. What are the relationships among the Schizaeaceae sensu lato? Do they form a monophyletic group, and, if so, should we recognize three families, only distantly related, with the Anemiaceae and Lygodiaceae separated?

13. Are the Pteridaceae (and Vittariaceae) most closely related to or derived from the Schizaeaceae, as many have suggested, or are they more closely allied to the higher leptosporangiate ferns? Is the segregate family Vittariaceae derived from the Pteridaceae, as usually suggested, and if so, what is its progenitor? Is it *Adiantum*?

14. Are the Dennstaedtiaceae allied with the Dicksoniaceae, as some have postulated, or are they part of a higher leptosporangiate clade, ancestral to, or an early offshoot from the line leading to the dryopteroids, asplenioids, and blechnoids? Are the lindsaeoid ferns properly placed in the Dennstaedtiaceae, or do they form a separate, phyletically isolated lineage?

15. What is a reasonable circumscription of Dryopteridaceae, the limits of which are the subject of perhaps the greatest disagreement among fern systematists? Are the various segregates (Oleandraceae, Onocleaceae, Davalliaceae, Nephrolepidaceae, Lomariopsidaceae, etc.) sufficiently distinct and monophyletic, or are they polyphyletic assemblages united mainly by character states, such as dimorphism in Lomariopsidaceae, that we know have arisen many times?

16. Do the higher leptosporangiate families, including Aspleniaceae, Blechnaceae, Davalliaceae, Dryopteridaceae, Thelypteridaceae, Polypodiaceae, Grammitidaceae, Pteridaceae, and perhaps even Dennstaedtiaceae, (the old Polypodiaceae sensu lato), form a clade, or do they have separate origins from among the more primitive ferns? That is, are they, as some suggest, all more closely related to each other than to any of the more primitive ferns?

These questions and more are our challenges. Our goal should be to address and answer as many of them as possible. Experience suggests that resolution of genealogical questions requires utilization of data from many sources. These sources should include the traditional ones, monographs of genera and families, as well as broad comparative studies of morphological and anatomical characters; indeed, we must improve on and add to this body of evidence. But the morphological evidence should be complemented by new sources of data, molecular, developmental, paleobotanical, and others yet unknown. As we progress in assessing kinship, we are likely to be able to pose many more intriguing questions, and thus gain insight into the evolutionary history of the ferns.

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